ALLOMETRY AND HETEROCHRONY IN THE GROWTH OF THE NECK OF TRIASSIC PROLACERTIFORM REPTILES

by KARL TSCHANZ

ABSTRACT. The functional morphology of the elongated neck of *Tanystropheus longobardicus* (Bassani) has long been controversial. It is suggested here, that the neck was not very flexible because the elongated cervical ribs are bundled along the ventrolateral margin of the vertebrae. The result, a stiffened neck, is advantageous in an aquatic environment. The ontogenetic development of the neck in *T. longobardicus* and *Macrocnemus bassanii* Nopcsa, both included within the Prolacertiformes, is another point of interest. During ontogeny, the neck exhibits constant, positive allometric growth with differing growth parameters for the two taxa. This difference most likely resulted from heterochronic processes. The marked elongation of the neck in *T. longobardicus* was primarily caused by hypermorphic growth. Additional factors, modifying the growth pattern, include predisplacement of growth and an increased number of cervical vertebrae.

THE monophyly of the Prolacertiformes is corroborated by a number of synapomorphies, such as an incomplete lower temporal bar, elongated cervical vertebrae, low neural spines on the cervical vertebrae, and a short ischium (Benton 1985). It includes the taxa *Prolacerta, Macrocnemus, Tanystropheus, Tanytrachelos* (Olsen 1979; Wild 1980*b*; Benton 1985), and possibly *Protorosaurus* (Carroll 1981; Benton 1985). Other taxa like *Cosesaurus* (Olsen 1979) and *Malerisaurus* (Chatterjee 1980) have been included in the Prolacertiformes, but their relationship is not firmly established. A characteristic feature of the Prolacertiformes is their elongated neck. The elongation results mainly from lengthening of the cervical vertebrae. An increase of their number occurs in some taxa, adding to the elongation of the neck. The shortest relative length of the neck is observed in *Prolacerta* (8 cervical vertebrae); it increases slightly in *Macrocnemus* (8 cervical vertebrae) and markedly in the most advanced species of *Tanystropheus* (9–12 cervical vertebrae). In adult *T. longobardicus* the cervical vertebral column equals more than half of the total body length.

The earliest interpretation of the elongated neck vertebrae of *Tanystropheus*, from the Triassic Muschelkalk Beds of Germany, was by Münster (1834) who believed them to represent elements of dinosaur extremities. In 1855, H. von Meyer interpreted the same bones as caudal vertebrae of a dinosaur which he named *T. conspicuus*. The most unconventional hypothesis has been proposed by Nopcsa (1923), who considered the elongated bones as wing elements (phalanges) of a pterosaur (*Tribelesodon longobardicus* Bassani). Apparently only poorly preserved material from the Grenzbitumenzone Beds of Besano (northern Italy) was available to Nopcsa. The discovery of a complete skeleton of a reptile with an elongated neck in the Grenzbitumenzone Beds from Monte San Giorgio (Switzerland) by Peyer in 1929 finally revealed the true identity of the elongated bones as cervical vertebrae of *Tanystropheus longobardicus* (Bassani). Systematic excavations in the Middle Triassic Grenzbitumenzone of Monte San Giorgio (Switzerland) yielded about fifteen fairly complete skeletons of *T. longobardicus* (Wild 1973).

FUNCTIONAL MORPHOLOGY

Ever since the first discovery of a complete skeleton, the life style of *T. longobardicus* has remained enigmatic. According to Peyer (1931) *Tanystropheus* was a terrestrial animal. This view was based on morphological characters such as the form of the pelvic girdle, the presence of claw-like terminal

phalanges, and the proportions of metatarsals and metacarpals. Consequently, his reconstruction shows *Tanystropheus* in a terrestrial environment. Locomotion was supposed to have been clumsy, not more than a slow crawling. The short limbs may occasionally have supported locomotion which was effected mainly by lateral undulations of the vertebral column. Normally the body was thought to have lain directly on the ground, and the neck was oriented more or less horizontally.

A neck with a degree of flexibility comparable to that observed in birds (Boas 1929) was assumed by Peyer (1931). He therefore subdivided the neck of *T. longobardicus* into parts of different mobility. But the compartmentalization was not considered to be as advanced as in birds. Nevertheless, the elongated neck could have been used as a perfect instrument to grasp highly mobile prey. Sitting safely near the shoreline, *T. longobardicus* was believed to be able to snap at fishes (text-fig. 1*a*). One problem, the phylogenetic development of the elongated neck of *Tanystropheus*, remained enigmatic to Peyer (1931). He postulated that this development would not have been possible if *Tanystropheus* had always lived in a terrestrial environment. This is why the hypothetical ancestor was thought to have been at least partly aquatic.

Wild's (1973) description of *T. longobardicus* was based on a sample of twenty-seven nearly complete specimens from the Swiss part of the Grenzbitumenzone Beds, and on some isolated, cervical vertebrae of *T. conspicuus* recovered from the German Upper Muschelkalk. Interpretation of the mobility of the neck was based on a detailed analysis of the position of the zygapophyses. Some of Peyer's (1931) hypotheses were confirmed, e.g. the subdivision of the neck into three parts of different mobility. The cervical ribs, even more elongated than the cervical vertebrae, were supposed to be elastic and to protect the blood vessels, the trachea, and the oesophagus. In addition, the ribs supported the elongated neck at the intervertebral joints. Wild (1973) postulated that the neck was very flexible. When on land, the neck of *T. longobardicus* would have been relatively elevated, and an S-shaped posture would have resulted (text-fig. 1*b*). Adult specimens show some adaptations to an aquatic life, as indicated by the proportions of fore and hind limbs. Together with the characteristic tooth replacement, this would be evidence for ecological changes during the life of *T. longobardicus*. According to Wild (1973, 1980*a*, *b*), the juveniles of *Tanystropheus* lived as terrestrial insectivores (tricuspid teeth), whilst the adults lived as aquatic carnivores (recurved, conical teeth). Stomach contents of adult *T. longobardicus* have yielded unquestionable hooks from cephalopod arms (phragmoteuthids) (Wild 1973).

Kummer (1975) reconstructed the position of the neck of *T. longobardicus*, according to fundamental static constraints. He concluded that the neck could not have been held horizontally without tilting of the animal. Consequently, his reconstruction shows *T. longobardicus* with the neck strongly recurved in a swan-like position (text-fig. 1*c*). This position appears advantageous if static constraints are considered in isolation. The shear stress on the cervical column resulting from this position would be minimal (Preuschoft 1976).

In this study (see also Tschanz 1986) the anatomy of the cervical vertebrae of *T. longobardicus* was compared with that of recent lacertilians. The following structural differences were recorded: reduced neural spines result in reduced attachment areas for important parts of the cervical musculature. Only the short, intervertebral muscles had extensive insertional areas. The musculature was too weak to lift the neck beyond the horizontal to the curved position postulated by Wild (1973) or Kummer (1975). The muscles would not only have had to counteract gravitational forces, but also to bend the cervical ribs dorsally. The ribs, slender and longer than the cervical vertebrae, are assumed to have been bundled (text-fig. 2). In this way they acted as two rods, lateroventral to each side of the cervical column. The cervical ribs are thickened at the intervertebral joints. The stiffened rods supported the vertebral column and would have reduced gravitational shearing stresses. This construction restricted dorsal bending of the neck of *T. longobardicus* (Tschanz 1985, 1986). Therefore, the reconstructions of *Tanystropheus*, given by Wild (1973) and Kummer (1975), with S-shaped or swan-like curved necks, have to be rejected. If *T. longobardicus* was capable of a terrestrial life, its neck would have been held out horizontally (text-fig. 1*d*).

In an aquatic environment the same neck construction would appear more advantageous. Relief for the musculature would have resulted from the buoyancy of the surrounding medium. Therefore,
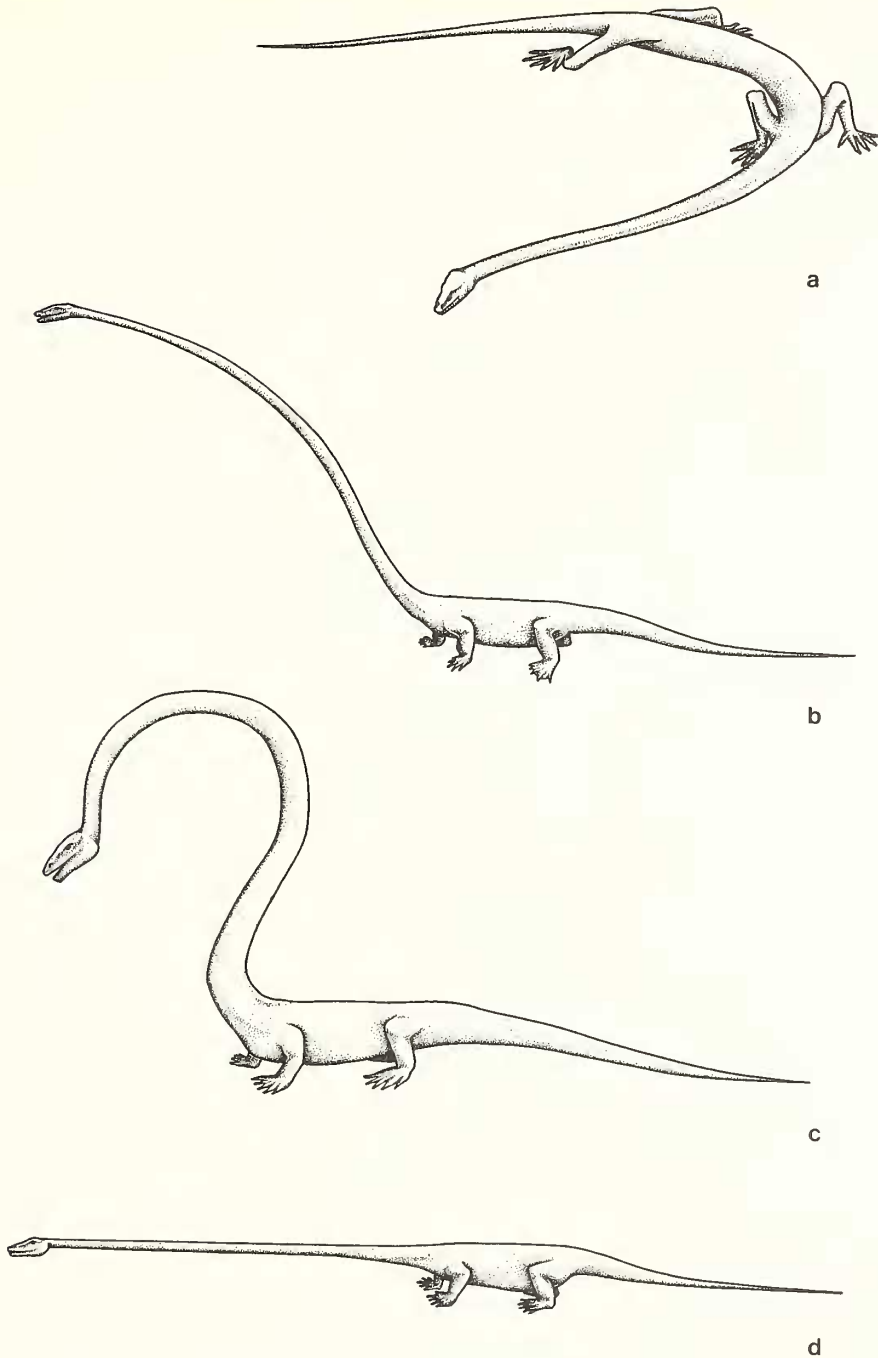
TEXT-FIG. 1. Different reconstructions of *Tanystropheus longobardicus. a*, as a mainly terrestrial reptile (redrawn after Peyer 1931). *b*, as a terrestrial reptile, with its neck in a 'normal', elevated position (redrawn after Wild 1973). *c*, with the neck in a swan-like position. If the head is positioned more forward the animal is supposed to tilt (redrawn after Kummer 1975). *d*, with the neck in horizontal position. This represents the most advantageous position for terrestrial and aquatic life (Tschanz 1985, 1986).
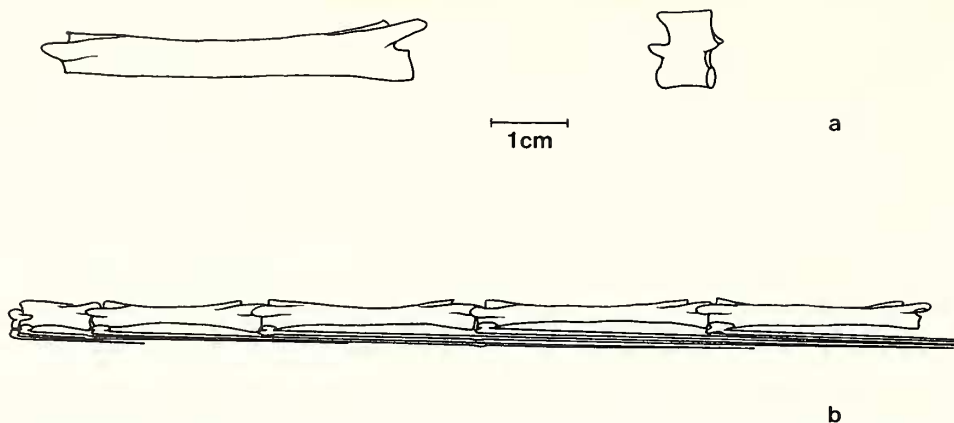
TEXT-FIG. 2. *a*, tenth cervical and last dorsal vertebra compared (specimen T2791). *b*, reconstruction of the rib arrangement in the anterior part of the neck in *Tanystropheus longobardicus*. The neck is supported by the elongated ribs.

the musculature counteracting gravitation would not have to be as extensive as for an animal with a terrestrial mode of life. In addition, a stiffened neck would have been advantageous for aquatic locomotion. Propulsion in *Tanystropheus* most likely resulted from lateral undulations of trunk and tail. The extension of these undulations forward beyond the trunk was restricted by the stiffened neck. Additionally, lateral bending in the region of the neck–trunk transition must have been prevented by the musculature of the shoulder girdle region. This enabled *T. longobardicus* to hold its skull straight in the direction of locomotion. At any rate, *T. longobardicus* with its reduced cervical musculature and its stiffened neck, was adapted to an aquatic environment. A more interesting question, however, addresses the growth parameters which would have created the elongation.

DEVELOPMENTAL PROCESSES

According to Wild, the elongation of the neck results from pronounced positive allometric growth relative to absolute body size (as represented by the length of the precaudal vertebral column). A linear regression line could be fitted approximately to the point cluster of the logarithmically transformed length measurements of the cervical vertebral columns. This regression line is supposed to show two sharp breaks in its slope (text-fig. 3). For the first increase in slope no explanation was found. The second increase was correlated by Wild with sexual maturity in *T. longobardicus*, at an overall body length of about 2 m. This hypothesis seems reasonable because the regression lines of other elements (radius, humerus, skull) show a similar pattern of slope change at the same body size (Wild 1973, p. 138) (text-fig. 3). In addition, a characteristic pattern of tooth replacement, from tricuspid to conical, takes place at this time.

Another hypothesis explaining slope changes is that the sample contains specimens of two species with different body size. Different slopes of the regression lines then would reflect differential growth rates of the neck in these two species. This paper will concentrate on the analysis of the ontogenetic growth of the neck in *T. longobardicus* and the closely related, contemporary *Macrocnemus bassanii*. A basic premiss is that the studied specimens of *Tanystropheus* belong to a single species, *T. longobardicus*. The following hypotheses are tested: 1, ontogenetic growth of the cervical vertebrae of *T. longobardicus* and *M. bassanii* is positively allometric relative to absolute body size and remains constant during growth; 2, linear regression lines fit the data best and the allometric parameter b (slope of regression line) is equal for all the cervical vertebrae of one taxon;
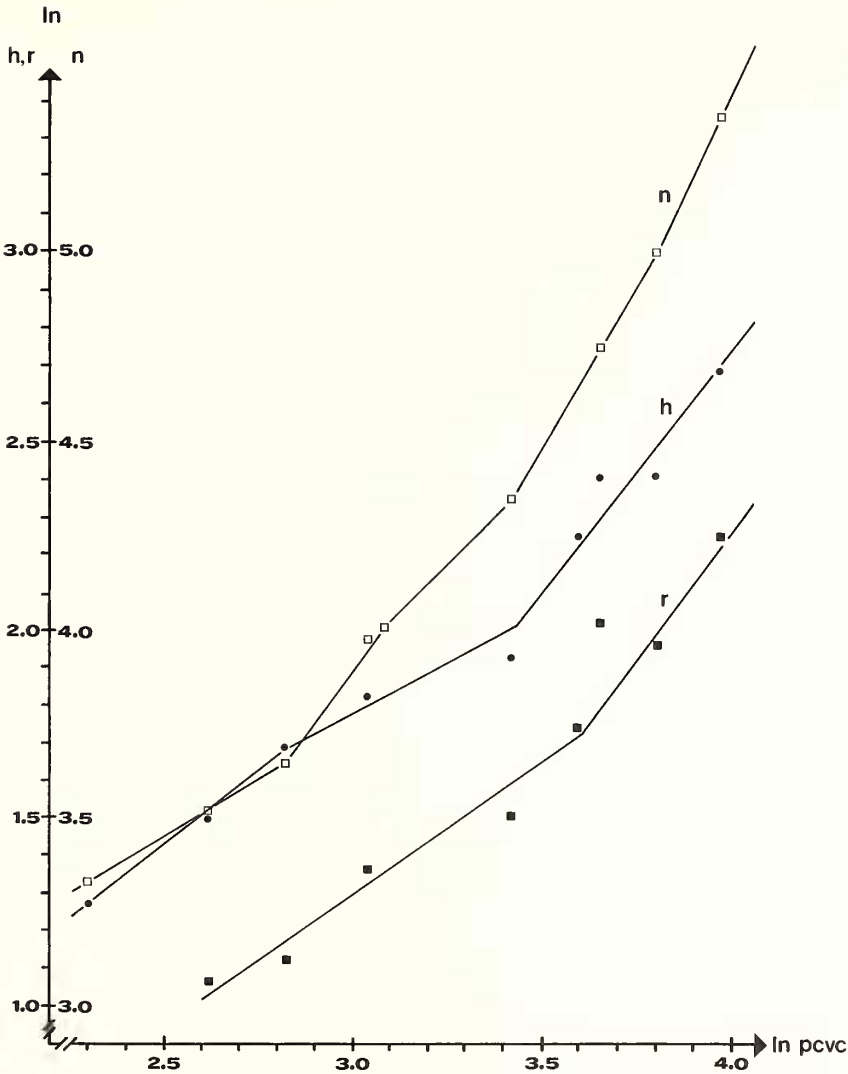
TEXT-FIG. 3. Approximately fitted regression lines of the neck (n), humerus (h), and radius (r) versus precaudal vertebral column (pcvc) in *Tanystropheus longobardicus*. The regression lines show sharp breaks in slope (redrawn after Wild 1973).

3, the allometric growth of the neck in *Tanystropheus* and *Macrocuemus* is comparable. The pattern in *M. bassanii* represents the pattern of a hypothetical ancestor of *T. longobardicus*.

The last hypothesis is supported by the fact that some characters of *M. bassanii* are not as advanced as in *T. longobardicus*, especially in the cervical vertebral column. The cervical column of *M. bassanii* consists of only eight cervical vertebrae with relatively high neural spines, and the cervical ribs are relatively short. A similar pattern is shown by *T. antiquus*, stratigraphically the oldest representative of the genus *Tanystropheus*. Its neck consists of nine cervical vertebrae, and they are more elongated. It is possible to establish the polarity of evolution within the Prolacertiformes, based exclusively on morphological and growth characters of the cervical vertebrae.

Prolacerta shows the most primitive condition in neck elongation. The eight cervical vertebrae are only moderately elongated and possess high neural spines. *M. bassanii* retains the primitive number of cervical vertebrae but they are more elongate than in *Prolacerta*. The neural spines are relatively high. *T. antiquus* shows similarly built cervical vertebrae, but additionally a ninth vertebra is included in the series (Wild 1987). In the most advanced forms, *T. longobardicus* and *T. conspicuus*, the cervical vertebrae are more elongated and their number is increased to twelve. The two species possibly have to be unified within a single species pending the discovery of cranial material (Wild 1980*b*). *Tanytrachelos*, a small prolacertiform from the Upper Triassic of North America, is allied to *Tanystropheus* as it shares the same number of cervical vertebrae, although these are not as elongate. If *M. bassanii* is the hypothetical ancestor of *T. longobardicus* it would be possible to analyse ontogenetic growth of the latter in terms of heterochronic processes. Phylogenetic and/or ecological implications of the elongated neck of the Prolacertiformes may hence be inferred. At any rate, the effects of ontogenetic change on growth pattern will be better understood. In particular, structures with no recognizable adaptive value may be more reasonably explained as results of allometric growth.

MATERIAL AND METHODS

Most specimens of *T. longobardicus* and *M. bassanii* on which this study is based come from the Middle Triassic Grenzbitumenzone (Anisian/Ladinian) and one specimen of *M. bassanii* comes from the Lower Meridekalk (Ladinian). The specimens were found at several localities on the Monte San Giorgio (Switzerland). They are housed at the 'Paläontologisches Institut und Museum der Universität Zürich' (Table 1).

The allometric analysis is exclusively based on specimens with a partially preserved trunk region. These were eight specimens of *T. longobardicus* (two with complete cervical column) and five specimens of *M. bassanii*. Most specimens lack one or more cervical vertebra, or they are incompletely preserved. Measurements were taken of the lengths of the centra of all cervicals, a middle dorsal vertebra, and the last presacral vertebra. A slide caliper with mm scaling was used to a degree of accuracy of ± 0.5 mm (Tables 2 and 3). If one end of a vertebra was incomplete, the total length of the centrum was extrapolated.

TABLE 1. List of the analysed specimens.

Specimen	Stratigraphy	Status of preservation
Tanystropheus longobardicus (Bassani)		
T1277	Grenzbitumenzone	Disarticulated skeleton, only posterior cervicals preserved
T2482	Grenzbitumenzone	Disarticulated skull and anterior cervicals, last presacral vertebra not preserved
T2485	Grenzbitumenzone	Disarticulated skeleton, only posterior cervicals preserved
T2787	Grenzbitumenzone	Disarticulated but nearly complete skeleton
T2791	Grenzbitumenzone	Complete skeleton, anterior cervicals disarticulated
T2795	Grenzbitumenzone	Disarticulated skeleton, cervicals partly in sequence
T2817	Grenzbitumenzone	Skull and anterior cervicals missing, posterior cervicals poorly preserved
T2818	Grenzbitumenzone	Complete skeleton
Macrocnemus bassanii Nopcsa		
T2472	Grenzbitumenzone	Articulated, nearly complete skeleton
T2476	Grenzbitumenzone	Cast of the specimen Besano 2 (Peyer), disarticulated, incomplete skeleton
T2815	Grenzbitumenzone	Disarticulated, incomplete skeleton
Cava Tre Fontane (CTF)	Grenzbitumenzone	Articulated, nearly complete skeleton
Alla Cascina (AC)	untere Meridekalke	Articulated skeleton, anterior part of the trunk and posterior cervicals missing

TABLE 2. Length (in mm) of the vertebrae of *Tanystropheus longobardicus* (Bassani).

	cerv. 2	cerv. 3	cerv. 4	cerv. 5	cerv. 6	cerv. 7	cerv. 8	cerv. 9	cerv. 10	cerv. 11	cerv. 12	m.dors.	l.dors.	neck
T2791	9·0	24·0	29·5	30·5	ap 30·0	ap 32·0	ap 40·0	50·0	45·0	26·0	ap 13·0	10·0	7·0	329·0
T2795	ap 11·0	28·0	36·0	ap 37·0	37·5	ap 42·0	50·0	57·0	54·0	34·5	ap 14·0	11·0	*8·0	401·0
T2482	14·0	41·5	52·0	52·0	*44·5	*48·0	*56·0	*67·5	*65·0	*48·0	*17·5	ap 13·0	*9·5	*506·0
T2485	*16·5	37·0	*55·0	*56·5	50·0	*58·0	64·0	77·0	75·0	49·0	16·0	ap 14·0	ap 11·0	*554·0
T1277	*18·5	*47·5	*61·0	*63·0	*60·5	62·0	67·0	83·0	90·0	67·0	30·0	ap 14·0	12·0	*649·5
T2787	35·0	89·0	108·0	110·0	109·0	113·0	132·0	*147·0	*146·0	91·0	*42·5	29·0	20·0	*1122·5
T2817	*40·5	*103·5	*131·0	147·0	ap 147·0	150·0	ap 160·0	*162·0	*161·5	*128·5	*47·5	30·0	22·0	*1378·5
T2818	67·0	170·0	ap 215·0	216·0	228·0	228·0	258·0	245·0	238·0	177·0	ap 70·0	*44·5	32·0	2112·0

ap: approximate length.
*: length calculated from regression lines.

TABLE 3. Length (in mm) of the vertebrae of *Macrocnemus bassanii* Nopcsa.

	cerv. 2	cerv. 3	cerv. 4	cerv. 5	cerv. 6	cerv. 7	cerv. 8	m.dors.	l.dors.	neck
Alla Cascina	7·0	12·0	12·5	12·0	11·0	10·5	*9·0	5·5	5·0	*74·0
T2472	*10·5	*17·5	20·5	20·5	19·0	16·0	13·0	7·5	7·0	*117·0
T2476	11·5	20·5	*21·5	ap 22·0	ap 20·0	*17·5	*14·0	8·5	ap 7·5	*127·0
T2815	ap 13·0	21·0	ap 24·0	23·5	ap 23·0	ap 19·5	*15·0	9·0	8·0	*139·0
Tre Fontane	12·5	20·0	23·5	23·5	23·0	20·0	16·0	9·0	ap 8·5	138·5

ap: approximate length.
*: length calculated from the regression lines.

The lengths were transformed logarithmically. Regression lines (reduced major axis) were then fitted to the point clusters produced by plotting the lengths for the cervical vertebrae versus the lengths of the last presacral vertebra (text-figs. 4–6). Reduced major axis was given preference over least squares because it operates symmetrically on the two variables (Imbrie 1956). Isometry for the relation length of the last presacral vertebra versus absolute body size (e.g. body weight) is required. The resulting allometric parameters b (slope of the regression lines) were subjected to statistical testing. Possibly undetectable distortions did occur because of the small sample size. Therefore, despite statistical significance, the value of confidence may be reduced. The total length of the cervical vertebral column was calculated as the sum of the lengths of the cervical vertebrae. The lengths of missing vertebrae were calculated, based on the particular regression line.

Analysis of longitudinal growth makes the definition of a standard measure for absolute body size necessary. The standard measure chosen by Wild (1973) was the total length of the precaudal vertebral column. This is inaccurate, however. First, the axial skeleton is usually incompletely preserved, and secondly, the vertebrae to be analysed are part of the standard length. Because it is usually well preserved, the last presacral vertebra was chosen for this analysis. Also this vertebra is easily identified. According to Currie and Carroll (1984), the length of the centrum of any other dorsal vertebra could serve as a standard as well. Indeed, it could be shown that growth of the last presacral vertebra proceeds isometrically relative to any other dorsal vertebra.

The functions in general use for quantifying allometric growth are power functions ($y = ax^b$). Logarithmic transformation therefore will result in regression lines with the function $Y = A + bX$. The parameter A (log a) corresponds with the intercept of the y-axis by the regression line. The parameter b (allometric coefficient) is the slope of the regression line. Growth is positively allometric with $b > 1.0$. The significance of the positive allometric growth was tested (z-test; $H_0 : b_{cerv} = b_{last\ dors}$) (Imbrie 1956). The regression lines were additionally tested to substantiate the hypothesis that they are members of the same cluster ($H_0 : b_n = b_{n-1}$), and therefore have to be treated as parallel lines.

RESULTS

Tanystropheus longobardicus

The regression analysis indicates that ontogenetic growth of the cervical vertebrae is strongly positively allometric. Correlation is high with coefficients (r) close to 1.00 (Table 4). Therefore, the point clusters are best represented by linear regressions (text-fig. 4). The values for the slopes of

TABLE 4. Reduced major axis slopes (b), standard deviations s_b, y-intercept (A), correlation coefficient (r) from the regression of log length of cervical vertebra on log length of last presacral vertebra for *Tanystropheus longobardicus*. If the z value of the test for equality of the slopes of the cervical vertebrae and the last presacral vertebra is > 1.96 the probability is > 0.05.

Vertebrae	b (slope)	s_b	A	r	z
m.dors.	1·04	0·06	0·08	0·983	
2	1·30	0·03	−0·14	0·999	3·71
3	1·28	0·07	0·29	0·992	2·67
4	1·26	0·06	0·43	0·995	2·75
5	1·27	0·12	0·43	0·975	1·77
6	1·33	0·12	0·34	0·975	2·23
7	1·27	0·02	0·44	0·999	3·83
8	1·22	0·05	0·56	0·995	2·25
9	1·05	0·02	0·80	0·999	0·17
10	1·09	0·04	0·75	0·997	0·71
11	1·18	0·13	0·53	0·964	1·00
12	1·19	0·15	0·08	0·961	0·64
neck	1·22	0·06	1·49	0·989	2·25
neck (1–8)	1·27	0·02	1·23	0·998	3·83
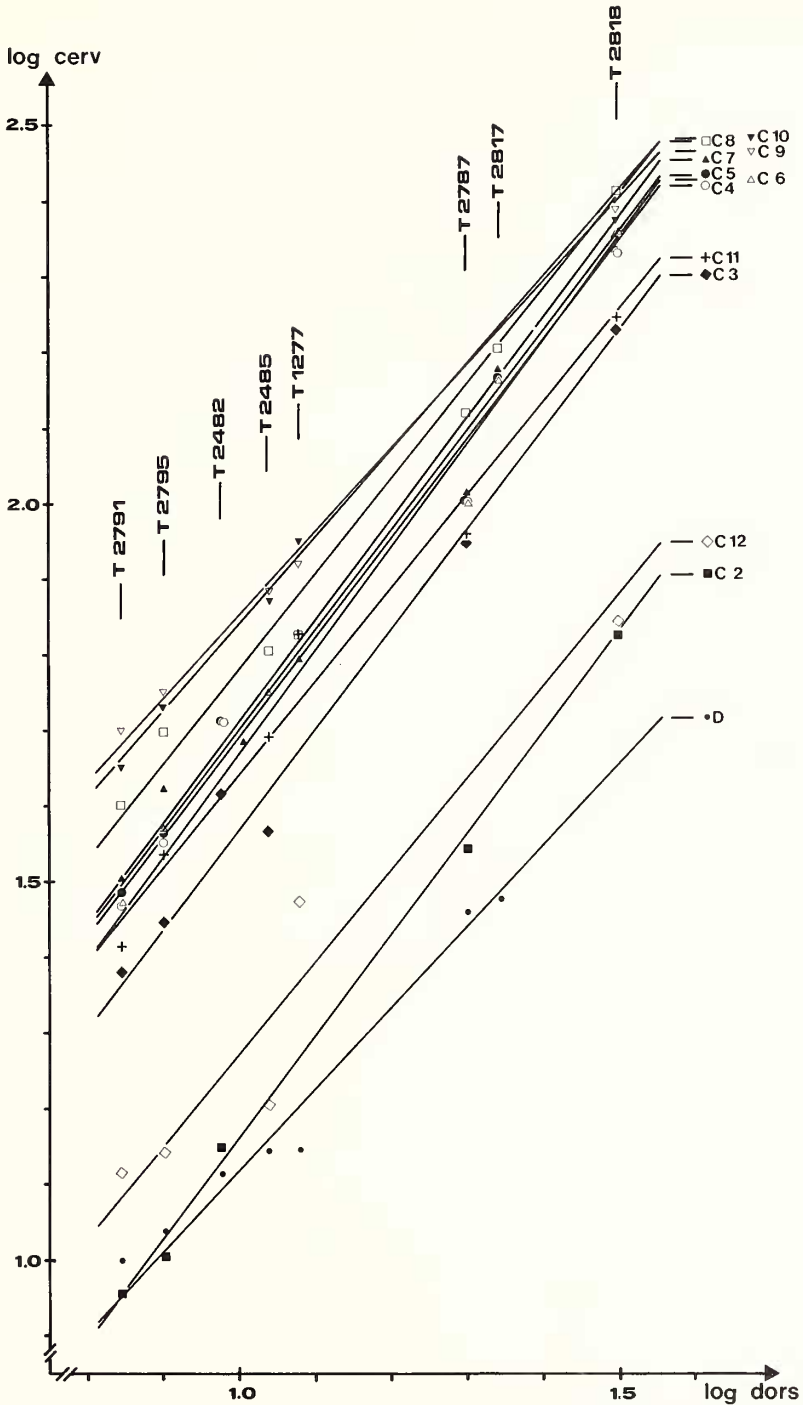
TEXT-FIG. 4. Reduced major axis for the cervical vertebrae (C2–C12) and a middle dorsal vertebra (D) of *Tanystropheus langobardicus*. log cerv = logarithmically transformed length values of the cervical vertebrae, log dors = logarithmically transformed length values of the last presacral vertebra.

the regression lines (parameter b) vary between 1.05 ± 0.02 (9th cervical vertebra) and 1.33 ± 0.12 (6th cervical vertebra) (Table 4). The hypothesis that growth is isometric ($H_0 : b_{cerv} = b_{last\ dors}$) has to be rejected for most cervical vertebrae (Table 4). Therefore, they grow in a significantly positively allometric fashion, with the exception of the cervicals 9 to 12. The cervical vertebrae 9 and 10 are the most elongated of *T. longobardicus*. Therefore, it is surprising that growth is not significantly positively allometric for these vertebrae. But it is possible that this is only an artifact of the small sample size (only five length values in each case).

The hypothesis of parallel regression lines ($H_0 : b_n = b_{n-1}$) cannot be rejected in most cases. The regression lines have thus to be treated as a bundle of parallel lines. The slope of the regression for the total neck length of *T. longobardicus* has a value of 1.22 ± 0.06 (Table 4; text-fig. 6). As expected, the ontogenetic growth is also positively allometric. To calculate this regression, the standard errors of the calculated lengths of missing cervical vertebrae have not been taken into account. Therefore, the standard error of the allometric parameter b would be higher than calculated (± 0.06).

Macrocnemus bassanii

The values of the allometric parameter b vary between 1.12 ± 0.14 (3rd cervical vertebra) and 1.47 ± 0.08 (6th cervical vertebra) (Table 5). The variability is greater than in *T. longobardicus*. Growth of all cervical vertebrae, except for the third, is significantly positively allometric (Table 5). The regression lines have to be treated as parallel lines, but the significance is not as strong as for the regression lines of *T. longobardicus* (Table 5; text-fig. 7). The growth of the cervical vertebrae of *M. bassanii* seems to have been accelerated as compared to *T. longobardicus* since the regression lines are steeper. The regression line of the total neck length has a slope (parameter b) of 1.27 ± 0.07 (Table 5; text-fig. 6). The difference from the slope of the regression line of the neck in *T. longobardicus* ($b = 1.22 \pm 0.06$) is not very spectacular, the ontogenetic growth of the neck of *M. bassanii* is slightly increased. The difference was not found to be statistically significant ($z_{M/T} = 0.56$). It is possible that this is again due to the small sample size. In addition, the size range of the five specimens of *M. bassanii* is not as great as the size range of the eight specimens of *T. longobardicus*.

TABLE 5. Reduced major axis slopes (b), standard deviation s_b, y-intercept (A), correlation coefficient (r) from the regression of log length of cervical vertebra on log length of last presacral vertebra for *Macrocnemus bassanii*. If the z value of the test for equality of the slopes of the cervical vertebrae and the last presacral vertebra is > 1.96 the probability is > 0.05.

Vertebrae	b (slope)	s_b	A	r	z
m.dors	1.00	0.03	0.02	0.997	
2	1.20	0.10	0.01	0.987	1.92
3	1.12	0.14	0.30	0.968	0.86
4	1.29	0.11	0.21	0.986	2.64
5	1.37	0.09	0.13	0.989	4.11
6	1.47	0.08	0.02	0.993	5.22
7	1.26	0.05	0.14	0.997	4.33
8	1.07	—	0.21	—	—
neck	1.27	0.07	0.99	0.993	3.38

TEXT-FIG. 5. Reduced major axis of the cervical vertebrae (C2–C8) and a middle dorsal vertebra (D) of *Macrocnemus bassanii*. log cerv = logarithmically transformed length values of the cervical vertebrae, log dors = logarithmically transformed length values of the last presacral vertebra.
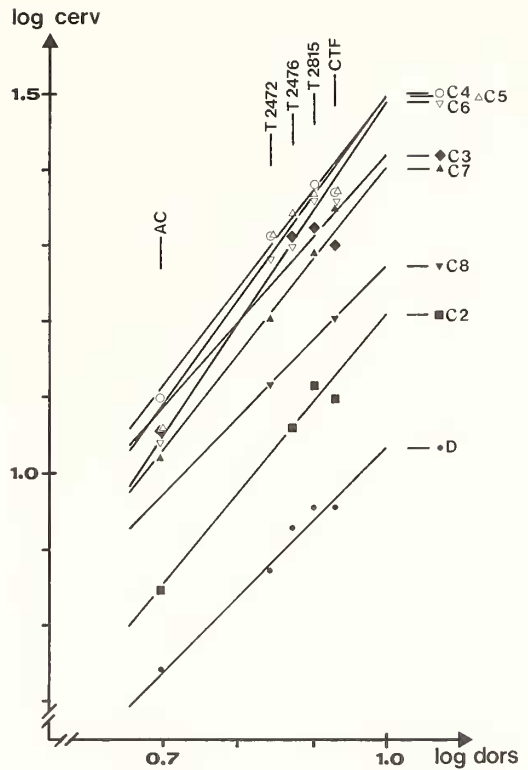
DISCUSSION

Evidence for positive allometric growth of the cervical vertebral column has been found in both genera analysed. Growth was constant during life (linear regression line). The two accelerations of the growth rate, as postulated by Wild (1973), one caused by unknown effects and the other by sexual maturity, could not be substantiated. No slowing of the growth rate (deceleration) could be observed for the largest specimens of *T. longobardicus*, in which the neck is relatively most elongated. Wild (1973) also postulated ontogenetic growth changes of the humerus and the femur (text-fig. 3). His data has been reanalysed too, and again linear regression lines resulted. The hypotheses formulated in the introduction, postulating unchanged positive allometry, are thus confirmed. The possibility remains that a larger sample size would result in modifications, but the fundamental trends are obvious.

Different allometric parameters b for the cervical vertebrae of *T. longobardicus* and *M. bassanii* indicate decelerated growth of the neck in the former taxon. Although this pattern is statistically unsubstantiated, it merits closer scrutiny. Decelerated growth of the neck of *T. longobardicus* can be explained by its body growth. It is possible that a structure with strong positive allometric growth will become functionally inappropriate or inadaptive if the same allometric growth parameter is maintained into a new size range (Gould 1966). Two strategies can be invoked to avoid loss of adaptation in structures generated by positive allometric growth:

a, decrease of the allometric parameter b (slope of the regression line),
b, decrease of the allometric parameter A (*y*-intercept).

Adult specimens of *T. longobardicus* are obviously much larger than adult specimens of *M. bassanii*; in other words the two taxa belong to different size classes. *T. longobardicus* can grow to

up to 6 m in length, while *M. bassanii* does not exceed a length of 1 m. Consequently, the decelerated growth of the cervical vertebrae of *T. longobardicus* can be correlated with increased body size. Decelerated growth indicates that the neck of *Tanystropheus* had reached an adaptive limit. Half of the total body length of a 4·5 m long animal was taken up by its neck. As explained above, the cervical musculature was not well developed in *T. longobardicus*. This would have caused functional restrictions of the neck if *Tanystropheus* had given rise to larger forms. The only way of bypassing the adaptive limit of neck growth with increasing body size would have been decelerated allometric growth of the neck.

Decelerated growth of the neck is caused by a decreased rate of morphological development. Decreased morphological development in the ontogeny of a hypothetical descendant indicates neoteny (McKinney and Schoch 1985). In other words, if the neck growth of *M. bassanii* corresponds with the neck growth of a hypothetical ancestor of *T. longobardicus*, the latter would show neoteny in relative neck length. Unfortunately the differences of slope could not be verified statistically.

Consequently, it is postulated that the extreme elongation of the neck in *T. longobardicus* results from accelerated body growth. This pattern of growth to a new size range is called hypermorphosis. Therefore, *T. longobardicus* could be no more than a hypermorphic *M. bassanii*. In a hypermorphic taxon the onset of sexual maturity has been retarded in relation to the hypothetical ancestor (McNamara 1986; McKinney 1986), in this case represented by *M. bassanii*. Because the cervical vertebrae grew over a longer period, an extremely elongated neck resulted from its positive allometry.

The hypothesis that *T. longobardicus* is no more than a hypermorphic *M. bassanii* neglects some observations, e.g. the different values for the parameter A (*y*-intercept) (text-fig. 6) and the different number of cervical vertebrae. Differences of the parameter A can be explained as a means of avoiding inadaptive elongation of the neck. If the resulting neck is relatively shorter in the descendant its functionality is retained. There are two possible ways of shortening the neck; either its development starts out from shorter primordia, or the onset of its development is delayed. The latter mechanism of paedomorphosis is called postdisplacement (McNamara 1986). Both of these explanations are not applicable to *T. longobardicus*. In comparison to *M. bassanii* the cervical vertebrae of *T. longobardicus* are not shorter but relatively longer, as is indicated by the higher values for the parameter A for the latter. The onset of morphological development starts earlier. This pattern is called predisplacement. The result is a prolonged period of growth of the cervical vertebrae and resulting in a longer neck.

The cervical vertebral column of *T. longobardicus* comprises twelve vertebrae, four more than in *M. bassanii*, and three more than in *T. antiquus* (Wild 1980a, b; Benton 1985; Wild 1987). *T. antiquus* is closely related to the other two taxa, but it comes from older sediments than *T. longobardicus*. The number of presacral vertebrae seems to be the same (24 to 25; Peyer 1937) in all three taxa. Wild (1973) advanced the hypothesis that the 1st dorsal vertebrae of an ancestral form had been transformed to cervical vertebrae in *T. longobardicus*. In other words, a backward shift of the shoulder girdle with simultaneous transformation of the vertebrae would have occurred during phylogeny. Assuming the hypothesis to be correct, this transformation would provide an additional explanation for the extremely elongated neck of *T. longobardicus*. It might seem possible that the addition of cervical vertebrae is more important for the elongation of the neck than are the other parameters, such as hypermorphosis and predisplacement. At any rate, the effect of the addition of vertebral elements should be detectable. If the regression analysis for the total neck length is performed including only the anterior eight cervical vertebrae, identity of the resulting regression line with that of *M. bassanii* is to be expected. However, the two regression lines only approach each other, but are not superimposed (text-fig. 6). Therefore, the extreme elongation of the neck of *T. longobardicus* can only partially be explained by the addition of dorsal vertebrae. Hypermorphosis and predisplacement as parameters of heterochronic change are more important.
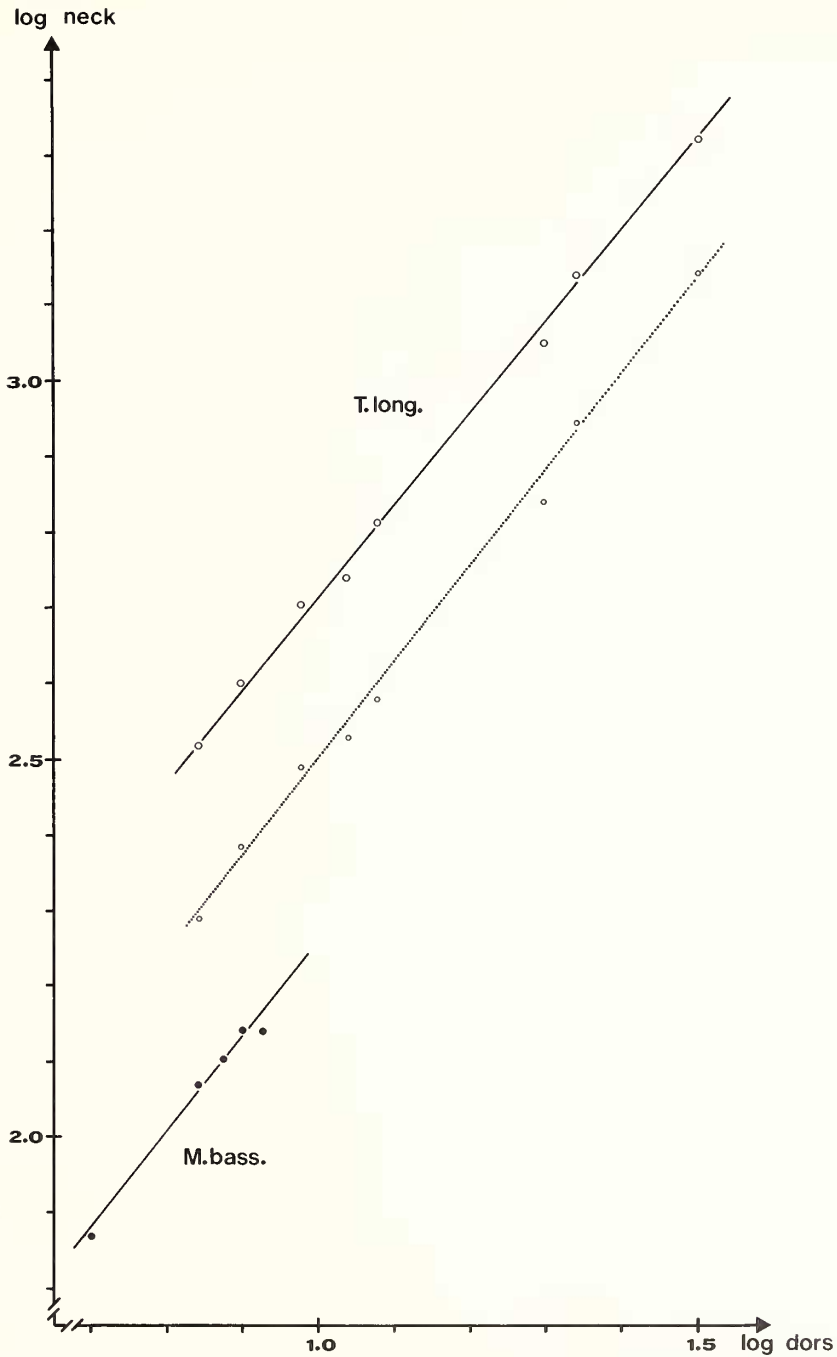
TEXT-FIG. 6. Reduced major axis of the neck of *Tanystropheus longobardicus* (traced line includes all the cervical vertebrae, dotted line includes only the anterior cervical vertebrae 2 to 8) and *Macrocnemus bassanii*. log neck = logarithmically transformed length values of the cervical vertebral columns, log dors = logarithmically transformed length values of the last presacral vertebra.

CONCLUSIONS

Reinvestigation of the growth of the cervical vertebrae of *T. longobardicus* and *M. bassanii* has shown that the elongation of the neck within the Prolacertiformes is caused by changes during early ontogenetic development and differences of adult body size. The hypothesis that all the studied specimens of *T. longobardicus* belong to a single species was confirmed because no evidence for ontogenetic changes of the allometric parameters has been found. The second hypothesis, dealing with constant positive allometric growth, has also been verified for both taxa analysed.

It is postulated that the elongation of the cervical vertebral column of *T. longobardicus* is caused by several processes of heterochronic change, characterized as peramorphic growth (McNamara 1986). All assumptions have been made relative to a hypothetical ancestor of *T. longobardicus*, with a morphology exemplified by *M. bassanii*. The most important cause for the elongation of the neck is hypermorphic growth, an evolutionary trend that occurs in the phylogenetic line of *T. longobardicus*. Other causes such as predisplacement and an increased number of cervical vertebrae have only a modifying character. It is supposed that in *T. longobardicus* the elongation of the neck had reached a point where further elongation would have produced a functionally impossible structure. Support for this hypothesis is given by the trend to reduce the allometric parameter b in *T. longobardicus*.

The hypothesis, that the evolution of the Prolacertiformes can be deduced from the development of the neck elongation, remains unresolved. More data would be needed about the ontogenetic growth in other taxa, such as *T. antiquus* Hühne, *T. meridensis* Wild, *T. fossai* Wild, *Prolacerta*, and *Tanytrachelos*. One form, *T. ahynis* Olsen, would be the most interesting to study. Approximately 100 specimens have been collected, which should form the basis for a successful statistical analysis of ontogenetic growth. On the other hand, *Tanytrachelos* is geologically the youngest prolacertiform known so far. In addition, this form remains very small. Therefore, it is possible that analysis of its ontogenetic growth would reveal a stronger positive allometry than for *Tanystropheus longobardicus*.

I propose that *T. antiquus* had a body size intermediate between *M. bassanii* and *T. longobardicus*. Its cervical vertebral column comprises nine cervical vertebrae, one more than *M. bassanii*, and these vertebrae are supposed to be more elongated. Recently, Wild (1987) reported a great number of complete skeletons of juvenile *T. antiquus* from the Black Forest. Until the description of this material, the intermediate position of *T. antiquus* remains open to question.

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KARL TSCHANZ

Paläontologisches Institut und Museum
der Universität Zürich
Künstlergasse 16
CH-8006 Zürich